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DEGRADATION OF PLANT REMAINS IN ORGANIC SEDIMENTS

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ONE of the least understood but at the same time fundamental processes which operates in nature is the alteration of plant residues into economically important substances such as peat, lignite and coal. In its broadest terms this degradation of plant substance must be regarded as a phase of the major organic cycle of carbon. It is obvious, however, that in "geologically permanent" large-scale accumulations of organic complexes such as the fossil fuels, we are concerned essentially with major deviations from, rather than participation in, the carbon cycle.

In a certain sense, therefore, the study of the accumulation of plant residues and their subsequent alteration comprise an area of botanical investigation which lies between microbiology on the one hand and the geological and chemical aspects of sedimentation on the other. Microbiological studies of degradation, however, are more often centered on specific organisms or on the metabolic products of their activity, rather than on an analysis of the effects produced on various naturally occurring substrata. In addition, emphasis in microbiological studies is quite logically placed more on the degradative aspects than on the accumulative aspects of the organic cycle.

The ultimate fate of organic residues in nature is determined in large part by diverse factors of the environment: physical, chemical and biological. The vast bulk of plant and animal remains is quite rapidly reduced, through complex energy-releasing processes, to simpler organic and inorganic compounds; and conversely, through complex energy-consuming processes these are re-incorporated into the tissues of living organisms. Conspicuously active and effective in the biochemical decomposition changes are the fungi and bacteria.

The rate of degradation due to microbiological activity is ordinarily most rapid in a warm, moist, highly aerobic environment. Favorable conditions are probably fulfilled to the greatest degree on or just below the surface of the soil. The ratio of accumulation versus degradation in the soil environment provides variable amounts of the so-called humus or organic component of the soil. If the environment is excessively wet, and more particularly if the availability of oxygen becomes deficient, the rate of degradation of plant tissues is greatly reduced. Such conditions reach their extreme in stagnant, poorly drained and relatively shallow basins such as swamps and bogs. Under such circumstances the accumulative phase exceeds the degradative phase and there results a gradual accretion of modified plant residues. In discussing the degradation and preservation of plant tissues it is therefore essential that reasonable distinction be drawn between environments in which aerobic microbiological changes may proceed at a rapid rate, as in soil, and subaqueous environments of submergence and oxygen deficiency. This distinction seems to be of fundamental importance since the character of the degradative changes is greatly influenced, if not primarily determined, by the degree of these contrasting conditions of the biological and physical environment. It might almost be said that

at one extreme of the spectrum of organic decay there are the various processes which operate in the soil and lead to the formation of soil organic matter, while at the other extreme there are the conditions of anaerobic submergence. In all cases microbiological processes induce physical and chemical changes in the plant tissues incorporated in the substratum, but the degree of change and the duration of the change vary profoundly.

Some understanding of the degradation of plant tissue is essential to a satisfactory interpretation of many types of plant fossils, since the variously modified remains of plant parts constitute the bulk of our knowledge of the paleontological record of plant life. For the most part these source materials are fragments or occasionally entire plants which fortuitously entered basins of deposition in which degradative processes were retarded and eventually inhibited. Under certain unusual and poorly known conditions the infiltration of mineral salts in solution and their subsequent precipitation resulted in an unusually perfect preservation of the original structure of the plant tissues. This is well known in the case of many fossil woods and other plant parts which are silicified or calcified. The sequence of events *preceding* mineralization, however, appears to have been basically similar to that which prevails in any accumulation of plant fragments, as in the formation of peat and other carbonaceous sediments. There seems to be no evidence that special environmental conditions have been responsible for the "biological fixation" of mineralized plant fragments, i.e., their unusual retention of organic structure. Rather, the unusual conditions have been those leading to precipitation of the mineral matrix itself, as in the calcareous nodules, or "coal balls," of certain coal seams, and the formation of silicified nodules.

In anticipation of the evidence to be shown later in

this paper, it may be stated here by way of a generalization that: (1) *The anaerobic degradation of the plant cell wall in sediments involves fundamentally similar structural changes in all plant tissues*; and (2) *These degradative changes are directly related to basic physical, chemical and structural features of the cell wall.*

The significant features in the general pattern of structural change in the anaerobic degradation of wood were described in a previous study of numerous woods recovered from an archeological site in Boston, Massachusetts (Bailey and Barghoorn, 1942). Since the publication of this earlier study, a far wider range of material from various geological horizons has been examined anatomically and, in part, microchemically. A more detailed description of these studies is in the course of publication (Barghoorn 1949),[1] but it seems desirable to review here the salient features of these investigations and their relation to various paleobotanical and anatomical problems as well as their possible bearing on dating archeological remains.

In wood of varying age, entombed in mineral or organic sediments, and permanently submerged, there occurs a gradual reduction of the amount of cellulose contained in the original unmodified cell walls. Depending on the availability of oxygen during degradative changes, and its effect on microbiological activity, a variable degree of "humification" results. Stumps of trees, submerged by sudden inundation, commonly occur embedded in peat deposits, yet may show little evidence of the "humification" so characteristic of the peat. For example, in the fresh water peats and "buried forests" of the

[1] As a section of the second monograph on the archeology, geology, stratigraphy and paleobotany of the Boylston Street Fishweir (Papers of the Robert S. Peabody Foundation for Archeology).

New England coast, now under tidal influence, numerous stumps and roots may be recovered which retain to a great extent the color of the original wood, yet whose tissues are altered to a soft, almost cheese-like consistency. Similarly, the permanently submerged basal parts of wooden piles driven into sediments in both marine and fresh water environments show a peripheral zone of degraded wood which may be relatively unchanged in color or gross appearance. Archeological remains of wood preserved in the anaerobic environment of estuarine sediments have been shown to undergo almost no "humification" or pronounced change from their original color (Bailey and Barghoorn, 1942). On the other hand, plant fragments from autochthonous peats or other organic accumulations in which aerobic degradation has played an important part almost invariably exhibit pronounced changes in color and the other physical and chemical modifications which feature the concept of "humification" (Waksman, 1938).

However, all degraded plant tissues, whether "humified" *or visibly* unaltered, are characterized by a significant reduction of their original cellulose, the extent of loss of cellulose being fundamentally an index of the degree of chemical and physical degradation. In view of these facts, which are well supported by numerous anatomical and chemical investigations (Mitchell and Ritter, 1934; Jurasky, 1938; Cartwright and Findlay, 1943; Waksman, 1938; Jahn and Harlow, 1942; etc.), it is of interest to examine in detail the structural changes which occur during degradation of the cell wall.

In order to orient the significance of these anatomical changes it is desirable to note briefly certain fundamental aspects of the structure of plant cell walls. Among higher plants the presence of a cell wall is the most conspicuous visible feature in the organization of tissues, organs and,

in general, of the entire plant body. The cell wall is composed initially, in its development from pre-existing cells, of a *primary wall.* This primary wall is a cellulosic layer (or series of layers) which ordinarily increases in surface area and may vary in thickness during the growth and enlargement of the cell. After growth and enlargement have ceased, a *secondary wall* may be formed, always internal to the primary wall. In many plant tissues, particularly in reproductive organs, secondary walls are not formed, and, in such cases the primary wall may become thick and conspicuous, comprising the bulk of the cell wall. In the cell walls of wood and woody plant tissues, however, thick secondary walls are ordinarily developed, the major topographic and structural feature of such tissues being their greatly thickened secondary walls.

The secondary walls of cells in woody tissues consist, except in certain cases, of three morphologically distinct layers or lamellae (Bailey and Kerr, 1935; Bailey, 1938; 1940). The innermost and outermost of these lamellae comprise relatively thin aggregations of cellulosic wall substance in which the crystalline cellulose aggregates tend to be oriented more or less transversely, or in helices of low pitch. The central and ordinarily thickest layer of the secondary wall, on the other hand, is composed most commonly of crystalline cellulose which tends to be oriented more nearly vertically, or in helices of steep pitch (Bailey, 1940). All three cellulosic lamellae may be infiltrated to varying degrees with encrusting substances such as lignin, terpenes, resins or other "protective" chemical complexes which retard biological and chemical degradation.

In the anaerobic degradation of wood it has uniformly been found that a consistent sequence of degradative changes occurs. This sequence shows a significant and fundamental relation to the lamellar structure of the cell

wall. The incidence of degradation of the lamellae is in the following order:

(1) Central layer of the secondary wall
(2) Innermost layer of the secondary wall
(3) Outermost layer of the secondary wall
(4) Primary wall[1]

Progressive stages in the deterioration of the cell wall are shown in Plates I–IV. Three outstanding features may be noted in these thin sections of degraded wood: (1) a reduction of the major portion of the secondary wall to a granular, virtually amorphous residue; (2) the retention of a structurally intact cell wall "layer" or "membrane" which corresponds in position to the primary wall; and (3) the presence of isolated or contiguous groups of cells whose secondary walls are relatively unaltered.

That the conspicuous granular remnants of degraded wall layers are essentially lignin residues may be demonstrated by their total extraction during delignification (compare Plate I, Figs. 1, 2 and 3 with Plate III, Figs. 1, 2 and 3). The visibly intact, persistent layers, or occasionally entire cell walls, are truly cellulosic, as may be shown by their brilliant birefringence in the microscope when viewed between crossed Nichols. Birefringence in the thinner cellulosic residual layers is greatly accentuated by delignification.

Because of their extremely tenuous character, certain structural residues, such as those in Plate I, Figs. 1, 3 and 4 and Plate III, Figs. 1, 2 and 3, might be assumed to consist solely of primary walls. The composition of these tenuous "membranes," however, can be shown to com-

[1] The term primary wall refers here specifically to the *wall layers* of individual contiguous cells exclusive of the true intercellular substance which is often erroneously, and confusingly, included as a part of the "primary wall" (Kerr and Bailey, 1934).

prise *five layers* viz., the outermost secondary wall layer and the primary wall of the two contiguous cells plus the true intercellular substance between the adjacent primary walls. The five-layered structure of these tenuous "membranes" is revealed by their relation to the pit border of bordered pit-pairs. This relationship is most easily observed in the late wood tracheids of coniferous woods, as shown in Plate III, Figs. 1, 2 and 3 (also compare Plate III, Fig. 3 with Fig. 5). The pit border is solely a structural feature of the secondary wall. It is apparent, therefore, that the tenuous innermost layer of the pit border, shown in Plate III, Figs. 2 and 3, is the resistant outermost or first formed layer of the secondary wall. Hence, it may be deduced that the persistent fraction of the cell wall in these tissues consists in large part of the remaining outermost layers of the secondary wall of two adjacent cells, including of course the retained and still more tenuous primary walls and true intercellular substance. That the persisting or visibly intact cell wall is actually a very minor part of the original unmodified secondary wall is shown in thin sections in which cells possessing intact secondary walls are intermingled with cells exhibiting extensively degraded secondary walls (Plate I, Figs. 1 and 2 and Plate III, Fig. 1). The reason or reasons for the retention of the *entire* secondary wall in certain cells which are in direct contact with others in which these wall layers are extensively degraded remain obscure.

It should be emphasized in connection with its greater resistance to degradation that the outermost or first formed layer(s) of the secondary wall possesses quite different staining reactions, optical properties and physical behavior from those of the broad central layer. The first formed layer is more heavily lignified than the central layer and shows far less tendency to swell in strong mineral acids, such as 72 per cent sulfuric acid or 40 per cent

hydrochloric acid. It is probable, therefore, that significant chemical as well as physical differences exist between the first formed and the subsequently formed lamellae of the secondary wall. In these respects the outermost layer of the secondary wall more closely resembles the primary wall than it does the later formed lamellae of the secondary wall.

The existence of a pronounced difference in the rate of degradation of the various cellulosic layers of a single cell wall presents a seeming paradox in the interpretation of cellulose decomposition. Two questions immediately arise: (1) what are the factors, biological or chemical, which cause the decomposition; and (2) what substance or substances impart such differential resistance to degradation within the cell wall itself? The fact that differential degradation of wall layers is not an isolated phenomenon, but instead a fundamental feature in the anaerobic decomposition of plant tissues emphasizes the significance of these questions and their bearing on the problem of cellulose decomposition in general.

In a previous study by the author these questions have been discussed in some detail, particularly with reference to environmental conditions and the possible causes of degradation (Barghoorn, 1949). It has been proposed, though not proven, that the degradation of wood deeply submerged in marine sediments is probably due in large part to the hydrolytic breakdown of cellulose rather than directly to microbiological attack.[1] It is probable, although again not proven, that the relatively high concentration of hydrogen sulfide (and associated hydro-sulfuric acid) in many carbonaceous marine sediments is responsible in part for the gradual chemical

[1] This conclusion does not question the apparently well established evidence confirming the existence of anaerobic bacteria at considerable depths in peat deposits (Thiessen and Strickler, 1934; Waksman, 1930).

hydrolysis of cellulose. Whether similar or comparable environmental factors are operative in terrestrial carbonaceous sediments remains to be determined.

The general uniformity of degradation in wood after prolonged submergence in sediments of diverse composition attests to the operation of a widely diffused set of factors which result in the gradual hydrolysis of the less resistant cellulosic fractions. In the case of the archeological remains previously noted it was found that wooden stakes, driven through successive strata of marine silt, peat and glacial blue clay, were uniformly degraded throughout, the physical condition of the stakes being identical in their entire length regardless of the surrounding media and the duration of submergence (Bailey and Barghoorn, 1942). Hence, the hydrolytic degradation of the cellulose appears to have progressed at an approximately similar rate regardless of the matrix. Similarly, entire stumps, logs or branches which have been submerged for periods exceeding thousands of years may become uniformly degraded and softened throughout, exhibiting no significant differences between their peripheral and interior parts. Occasionally the innermost portions of larger stumps may retain a core of intact or incompletely degraded wood. When freshly removed from its matrix the wood often shows little or no compression failure, nor even any significant change from its original volume; upon drying, however, it contracts excessively. Anatomical and chemical study shows that such degraded wood consists primarily of the lignin residue of the original wood substance, its cellulose content being reduced to a small fraction of the original, frequently on the order of three to five per cent. The persisting fraction of the cellulose, significantly, however, is found restricted primarily to those more resistant layers of the cell wall previously described. All of this evidence

indicates that gradual hydrolysis of the cellulosic matrix of the cell walls has proceeded at a rather uniform rate, the degradative changes first affecting the peripheral zone and slowly extending inward.

Ultimate complete degradation of the cellulosic framework of the wood cell wall may be delayed for enormously longer periods than have elapsed since the beginning of post-glacial time (Mitchell and Ritter, 1934; Jurasky, 1938; Barghoorn and Bailey, 1938). Recent extensive studies of lignites of Tertiary age show that in various genera of hardwood trees the lignitized wood retains from two and one half to six per cent of its original carbohydrate fraction, the major constituent of this fraction being degraded cellulose. In the same deposit lignitized fruits and seeds may show retention of as much as 45 to 50 per cent of their original carbohydrate fraction, predominantly cellulose.[1]

One aspect of the general problem which is of considerable theoretical, if not practical, interest is that dealing with the causes of selective retention of cellulose in certain lamellae of the cell wall. Two possible explanations for the selective degradation of cellulose are immediately apparent: (1) the presence in the cellulosic matrix of substances which effectively retard the hydrolysis (either microbiological or chemical) of cellulose; and (2) actual chemical differences in the cellulosic framework of the more resistant lamellae of the cell wall.

The first of these possible explanations finds much support from various observations and lines of evidence. For example, it has been established quantitatively by several investigators that the degree of lignification correlates with resistance to decay in wood and other woody tissues (Waksman and Cordon, 1936; Olson, Peterson

[1] Unpublished data from analyses of the Brandon lignite of Brandon, Vermont.

and Sherard, 1937; Virtanen, Koistinen and Kiuru, 1938). Additional evidence confirming the "protective" effect of lignin has been obtained by the author in a series of experiments utilizing a species of the cellulolytic bacterium *Cytophaga*. In a series of liquid cultures each containing mineral salts, filter paper and thin sections of various woods (*Pinus*, *Sequoia* and the hardwood *Trochodendron*), it was found that the filter paper was completely broken down within a period of a week, whereas the various wood sections were unaffected after six weeks incubation.

In addition to lignin, other normal constituents of the cell wall may serve to inhibit biological degradation of cellulose, viz., resins, terpenes and tanniniferous substances. Differential resistance of cell wall layers might logically be ascribed, therefore, solely to the effect of these encrusting "protective" substances of which lignin is undoubtedly the most significant in anaerobic degradation of woody tissues. In further support of this explanation of the selective breakdown of the cell wall, it should be emphasized that the most resistant layer of the secondary wall, viz., the outermost or first formed layer, is often far more heavily lignified than the broad central layer (Bailey and Kerr, 1935). Moreover, the primary wall, the most resistant of all the lamellae of the cell wall, is intensely lignified (Ritter, 1925; Kerr and Bailey, 1934).

The effect of degrees of lignification in different lamellae of the cell wall often produces striking morphological effects on the mode of attack of wood by various fungi. Fungi belonging to diverse genera of the Pyrenomycetes and Fungi Imperfecti commonly degrade wood by dissolving the central and often the innermost layers of the secondary wall, but leaving the outermost layer and the primary wall visibly unaltered (Bailey and Vestal, 1937;

Barghoorn, 1944). Early stages of this restricted breakdown of the cellulosic matrix are illustrated in Plate IV, Figs. 1 and 2, showing the invasion of wood by fungal hyphae. Similar in nature are the effects of certain brown rots on the degradation of wood. These are shown, perhaps more diagrammatically in Plate IV, Figs. 3 to 6. In some cases the entire secondary wall (with the exception of the tenuous outer layer) is completely removed, leaving a structural residue consisting of five layered "membranes" similar in composition to those previously described from wood degraded under anaerobic conditions (compare Plate III, Figs. 1 and 3 with Plate IV, Figs. 3, 4, 5 and 6).

All of this evidence indicates that the deterioration of wood is primarily a process of removal of cellulose, the rate of loss being, in many cases, significantly correlated with the degree of lignification or the protection of cellulose by other substances.

A fundamental exception to this relatively simple explanation, however, may be determined by an anatomical study of plant remains extracted from peats. In deflocculated, and subsequently delignified ("dehumified"), samples of fibrous peats innumerable delicate plant fragments are often released. In grass and sedge peats these fragments are most commonly cellulosic epidermal residues of roots and rhizomes. Microscopic examination often reveals preservation of even the most delicate epidermal structures such as root hairs, root cap cells and epidermal papillae (Plate VI, Figs. 1 to 6). Although these tenuous residues of roots have retained minute anatomical features in certain parts, they are devoid of their thick walled fibrous or conductive tissues (Plate VI, Figs. 1 and 2). However, in *undelignified* preparations of *comparable roots* there may be found degraded remnants of the originally thick walled conducting tissues

and fibers, whose secondary walls have been reduced to granular residues. The secondary wall residues and other degraded or "humified" decomposition products are readily extracted (with little or no deleterious action on the remaining cellulose) by means of various techniques utilizing sodium chlorite as the delignifying agent (Barghoorn, 1948).

Studies of fibrous peats of varying post-glacial age consistently show a cellulosic residue, often representing a very small fraction of the original sample. The amount of cellulose recovered is much influenced by the technique employed in lignin extraction; direct repeated chlorination or treatment with acidified hypochlorite solutions may result in oxidation and partial (or complete) solution of the persisting degraded cellulose residues. Anatomically, however, *structural cellulosic residues preserved in peats consist for the most part of thick, previously unlignified primary cell walls.* Tissues possessing thick, lignified secondary cell walls may undergo extensive degradation in environments in which even delicate cellulosic cell walls are incompletely broken down. In recognition of these facts it seems a paradox of note that the most delicate tissues of various plant organs may be far more resistant to anaerobic degradation than are cells or tissues possessing thick, frequently heavily lignified secondary cell walls.

In view of these observations, which are consistently supported by anatomical studies as well as by chemical analyses of degraded plant remains, it seems quite difficult to interpret selective degradation of different portions of the plant cell wall except in terms of chemical differences in the successively formed lamellae of the cell wall. In other words, *the exceptional resistance of the primary cell wall to degradation may be due to chemical rather than physical "protective" factors.* Such an inter-

pretation is strongly supported by the fact that primary wall cellulose often persists after degradation of the cellulose of heavily lignified layers of the secondary wall. For this and other reasons it seems difficult to interpret selective degradation of cellulose in different parts of the plant cell wall except in terms of chemical differences and resistance to hydrolysis in successively formed lamellae.

The persistence of the primary and occasionally the outermost layers of the secondary cell wall is strikingly shown in many silicified woods. Not uncommonly, silicified wood, regardless of geologic age, contains unusual amounts of organic residues, occasionally present to such an extent that the demineralized wood may be embedded, sectioned and stained much as living tissue (Arnold, 1931; 1941). In such material of diverse groups of plants which may range in age from Devonian to Tertiary, there is no cellulose remaining; it seems likely that silicification took place at a time when degradation of the cell wall had not yet passed the stage of the partial retention of a cellulosic structural residue. In other words, the cellulosic framework of the tissues was retained for a sufficient length of time to allow preservation of structure before silicification began. After or during the silicification process the remaining cellulose was lost from the tissue, leaving a modified but coherent lignin residue. This modified and silicified residue simulates the original cellulosic residue of anaerobically degraded wood (compare Plate I, Figs. 1 and 3 and Plate II, Figs. 2 and 3 with Plate V, Figs. 1, 2 and 5).

Whether the greater resistance to degradation of the cellulosic lamellae of the primary wall and the outermost secondary wall of plant cells is due to intrinsic chemical factors or primarily to physical protection by extraneous non-cellulosic substances cannot be determined without further coördinated histological and chemical study.

However, it is evident from anatomical and microchemical investigation that resistant fractions of cellulose occur in many organic deposits of various geologic ages and that these resistant fractions are directly related to predetermined structural features of the plant cell wall; hence they have their basis in the biochemistry of growth and differentiation of the cell wall.

Since the ultimate loss of cellulose in plant remains may, under certain conditions, be delayed to varying degrees for immense periods of geologic time, it is apparent that simple generalizations can scarcely be made regarding the complex processes of degradation in organic sediments as a whole. Chemical analyses of peat and humus have supplied data showing gross trends in the chemical alteration of plant remains in deposits (Waksman, 1938). However, such empirical analyses do not correlate microchemical and anatomical aspects of degradation, and in general they interpret natural decomposition of plant remains in terms of plant substance rather than in terms of the complex organization of cells and tissues. It is significant, however, that the less favorable the conditions are for microbiological processes, the greater is the retention of the original cellulose in plant accumulations. With increasing geologic age, total loss of cellulose occurs through "coalification" and various changes associated with the transformation of plant residues into higher rank coals. The problems of the earlier stages of cellulose degradation in anaerobic environments and of the processes of "humification" in general are in need of further coördinated anatomical, microbiological and chemical studies. Such investigations will be essential before a clear understanding of the major biological and chemical changes occurring between plant source materials and their geologic accumulation in the form of fossil fuels will be possible.

Summary

1. Alteration of plant residues under anaerobic conditions in organic sediments is a fundamental but inadequately known phase of the accumulation of carbon in nature.

2. Details of anatomical changes during decomposition of plant tissues are of importance in the morphological interpretation of many structurally preserved plant fossils.

3. Anaerobic degradation of the plant cell wall involves certain basic structural changes which appear to be similar in all plant tissues; these changes are directly related to basic physical and chemical features in the organization of the cell wall.

4. Degradation of the cell wall, either aerobically or anaerobically, is characterized primarily by loss of cellulose; the removal of cellulose most frequently follows a uniform sequence determined by the lamellar organization of the wall.

5. The incidence of degradation of cell wall lamellae in lignified tissues occurs in the following sequence:
    1. Central layer of the secondary wall
    2. Innermost layer of the secondary wall
    3. Outermost layer of the secondary wall
    4. Primary wall

6. The greater resistance of certain lamellae of the cell wall may be logically assigned to protection of the cellulosic framework by lignin and other "encrusting" substances. The persistence of unlignified primary walls in fibrous peats, however, cannot be explained by such mechanical protection, and demands an alternate explanation.

7. It is proposed, although it cannot be demonstrated within the scope of this study, that the greater resistance to hydrolysis of the primary wall and the outer secondary wall layer is due to chemical differences in the organization of the cellulosic matrix, rather than solely to a physical relation with lignin and other protective complexes.

8. The ultimate loss of cellulose in organic deposits may be delayed for periods measured in terms of geologic time, as shown by its presence in lignites of Tertiary and older age. The rate of loss, however, is greatly influenced by the initial biological conditions of deposition as well as by subsequent environmental changes accompanying "coalification."

9. Mineralization of plant remains apparently often occurs at a stage when cellulosic structural residues are still retained. Infiltration and precipitation of minerals, such as silica and calcium carbonate, occasionally cause a "fixation" of structure which, in mineral form, retains a large measure of biological detail. Such petrifactions may or may not retain a rather high percentage of the original, though chemically modified, organic matter during subsequent geologic change.

10. Many aspects of the problem of "humification" and "coalification" of plant residues are known only in empirical terms. An adequate understanding of these complex processes will necessitate extensive coördinated microbiological, anatomical and chemical investigation.

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ILLUSTRATIONS

EXPLANATION OF THE ILLUSTRATIONS

PLATE I. FIG. 1. Transverse section of the wood of a submerged white pine stump, age about 2000 years, showing differential degradation of the cell-wall. Note the presence of some intact cell walls, others incipiently degraded and many cells in which the secondary wall is largely reduced to a lignin residue occupying the center of the lumen. ×70.

FIG. 2. Transverse section of the same material showing incipient degradation of the secondary wall of an isolated tracheid (center) surrounded by cells in which the secondary wall has been largely degraded. ×170.

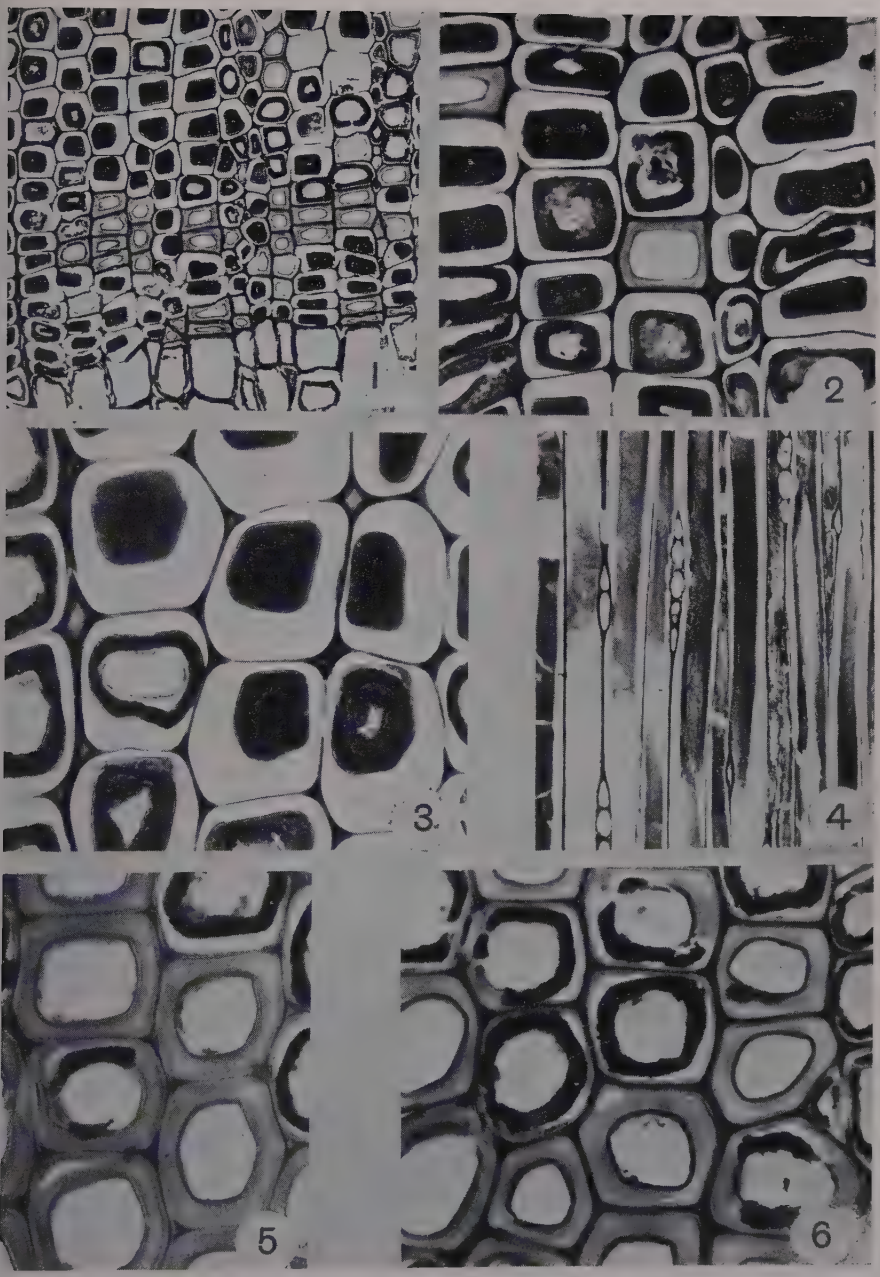
FIG. 3. Transverse section of the same, but more highly magnified. Note the discrete mass of the "coagulated" remnants of the major part of the secondary wall in the center of each cell. ×870.

FIG. 4. Tangential longitudinal section of the same material. The dark, heavily stained amorphous material represents the degraded remains of the central and inner layers of the secondary walls. ×100.

FIG. 5. Transverse section of a spruce pile, submerged in marine silt for 100 years. This section from the outer rings of the pile shows incipient degradation of the central and inner layers of the secondary wall. ×500.

FIG. 6. Transverse section from a different part of the white pine stump shown in Fig. 1. Note the complete breakdown of the central and inner layers of the secondary wall and the retention of the primary wall and the outermost layers of the secondary wall. ×500.

PLATE I



EXPLANATION OF THE ILLUSTRATIONS

PLATE II. Sections of wood of submerged white pine stump.
FIG. 1. Transverse section. Note the incipient degradation of the inner lamellae of the secondary wall of the tracheids, which shows compression wood, or "rotholz" structure. The heavily stained layers between the degraded inner lamellae and the less heavily stained outer secondary wall are non-cellulosic layers of the secondary wall. ×500.

FIG. 2. Transverse section. The visibly intact layers of the cell wall consist of the intercellular substance, primary wall and the outer secondary wall. The lignin residues of the central and innermost layers of the secondary wall form a discrete cylinder in the lumen of each cell. In this section, as also in Fig. 3, the outermost secondary wall is unusually thick and appears to consist of more than one layer. Undelignified, stained with Ruthenium red. ×800.

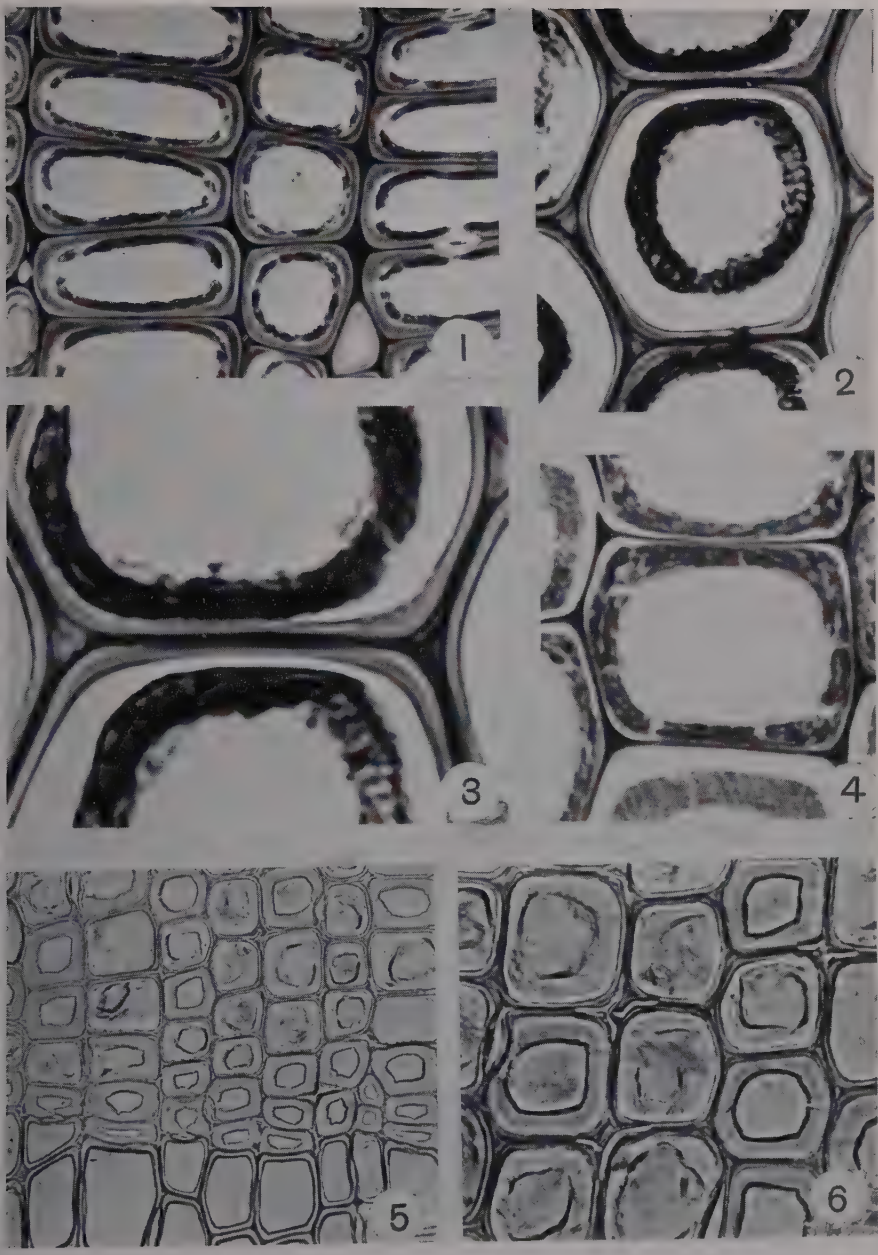
FIG. 3. Same section shown in Fig. 2, except more highly magnified. Undelignified, stained with Ruthenium red. ×1400.

FIG. 4. Transverse section showing varying extent of degradation of the secondary wall lamellae. ×800.

FIG. 5. Transverse section of less degraded wood from inner parts of the stump. Note the varying degrees of degradation of the secondary wall and the retention of a structural framework of modified cell walls. Unstained preparation. ×220.

FIG. 6. Same specimen as shown in Fig. 5, but from more extensively degraded wood. Unstained preparation. ×530.

PLATE II



EXPLANATION OF THE ILLUSTRATIONS

PLATE III. FIG. 1. Transverse section of wood of white pine stump. The section shows the cellulosic structural residue of degraded wood after extraction of lignin and lignin residues by sodium chlorite treatment. Four tracheids possess visibly intact secondary walls. All other cells are represented by walls consisting of intercellular substance, primary walls and *outermost* secondary walls. Stained with Ruthenium red. ×500.

FIG. 2. Same specimen as Fig. 1. The cellulosic structural residue consists of intercellular substance, primary walls and outermost secondary walls. Evidence for the presence of a secondary wall residue is provided by the persisting first formed layers of the pit borders. Delignified section stained with Ruthenium red. ×870.

FIG. 3. Same specimen as Fig. 1. Evidence that the cellulosic residue consists in large part of the outermost layer of secondary wall is shown by the conspicuous remnants of the borders of bordered pit-pairs. Note the retention of the pit torus. Delignified, stained with Ruthenium red. ×870.

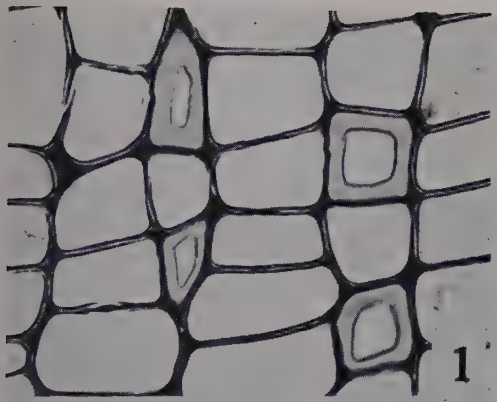
FIG. 4. Tangential longitudinal section of a degraded late wood tracheid of white pine showing the granular lignin residue of the secondary wall. Note the remnants of the bordered pit-pairs. Such cell wall residues, when delignified and viewed in transverse section, show the organization represented in Figs. 1, 2 and 3. ×500.

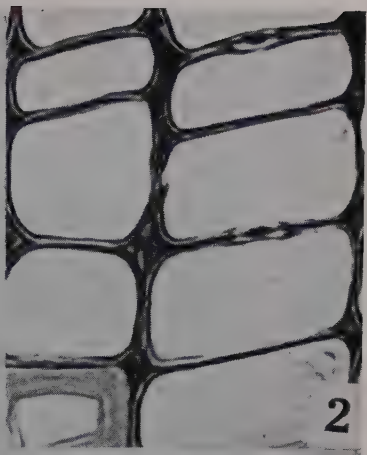
FIG. 5. Bordered pit-pairs of a normal spruce tracheid. Compare the lamellae with those shown in Figs. 2 and 3. ×870.

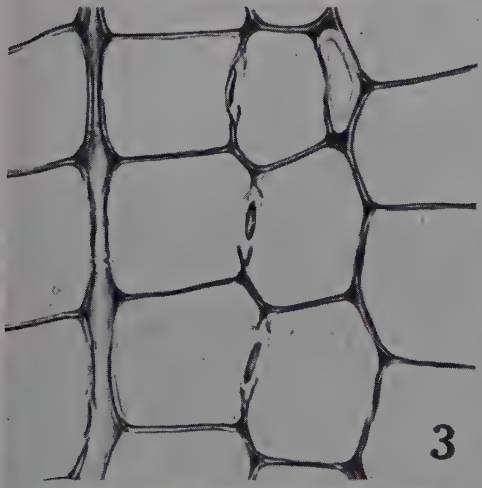
FIG. 6. Transverse section of "rotholz" of degraded white pine wood after treatment with 72 per cent sulphuric acid. The more heavily lignified primary walls and outer secondary walls yield a coherent structural residue comparable to that shown in Plate II, Figs. 2 and 3. ×800.

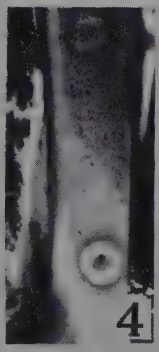
FIG. 7. Same specimen as shown in Fig. 6, but from different portion of the stump. Section treated with 72 per cent sulphuric acid. Note the lignin residue of the pit borders and compare with the cellulosic residue of the pit borders shown in Fig. 3. ×500.

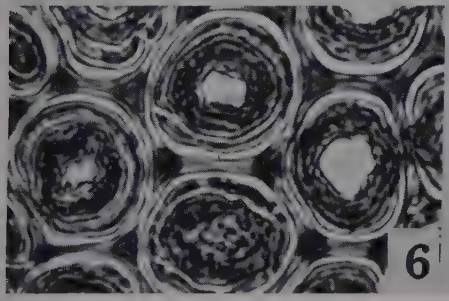
PLATE III











EXPLANATION OF THE ILLUSTRATIONS

PLATE IV. FIG. 1. Transverse section of xylem of *Laurelia aromatica* Juss., showing enzymatically produced cavities in the secondary wall. Note the partial localization of action within the central layers. (After Bailey, I. W. and Mary Vestal: Journ. Arnold Arboretum 28, Plate 209: 1937.) ×990.

FIG. 2. Transverse section of hard pine wood which was exposed to the sea and to the action of marine fungi. Enzymatic attack on the cell wall is concentrated within the central layers. Compare with anaerobic degradation as shown in Plates I, II and III. ×500.

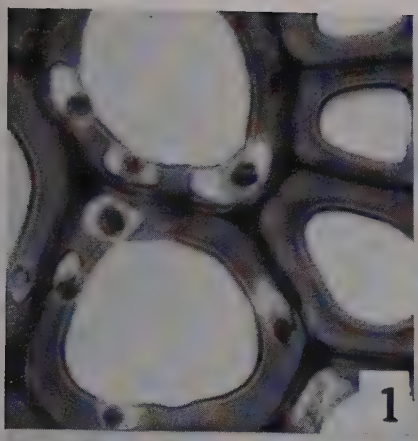
FIG. 3. Tangential section of xylem of *Ulmus crassifolia* Nutt. showing normal wood structure. ×100.

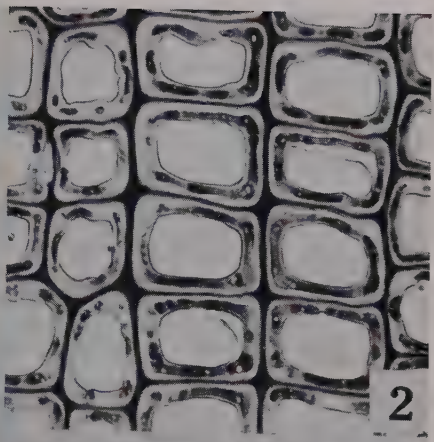
FIG. 4. Tangential section of xylem of *Ulmus americana* L. degraded by an unidentified brown rot fungus. The structural residue closely resembles delignified residues of anaerobically degraded wood as shown by comparison with Plate III, Figs. 1, 2 and 3. ×100.

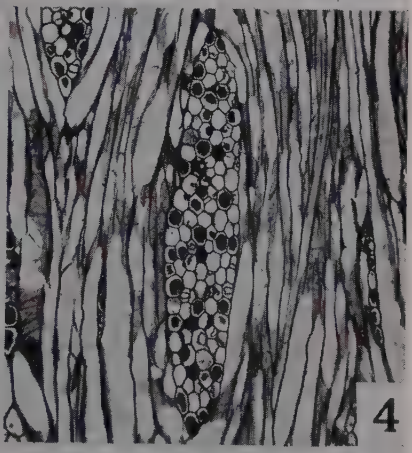
FIG. 5. Transverse section of xylem of *Ulmus americana* L. showing normal wood, with scattered gelatinous fibers. ×100.

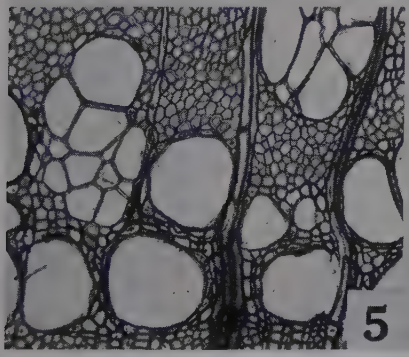
FIG. 6. Transverse section of xylem of *Ulmus americana* L. degraded by unidentified brown rot. Same specimen as shown in Fig. 4. The structural residue is lignified cellulose as shown by lignin extraction. ×100.

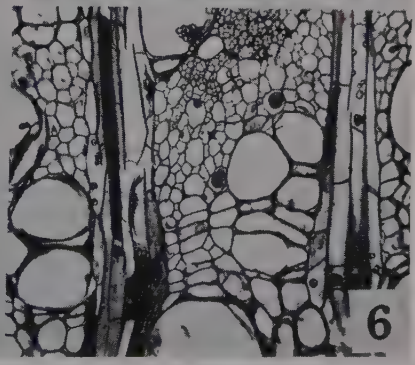
PLATE IV











EXPLANATION OF THE ILLUSTRATIONS

PLATE V. FIG. 1. Transverse section of an unidentified fossil wood of Cretaceous age. The wood is an intensely silicified organic residue of the original woody tissue. The cell wall layers retained closely resemble the cellulosic residues of anaerobically degraded wood as shown by comparison with Plates I and II. Ground section. ×132.

FIG. 2. Same specimen as shown in Fig. 1, but more highly magnified. Note the "lignin" residue of the secondary wall. ×732.

FIG. 3. *Robinia Pseudo-Acacia* L. Portion of vessel wall showing structure of the vestured pits. The vestured portion of the pit consists of primary wall. ×1532.

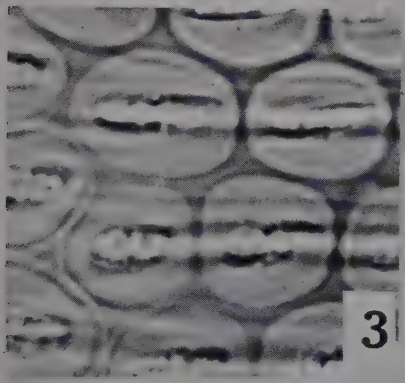
FIG. 4. *Robinia* sp. Silicified wood from the Tertiary of Montana. Portion of vessel wall showing retention of structure of the vestured pits. Compare with normal wood of *Robinia Pseudo-Acacia* L. shown in Fig. 3. Ground section. ×860.

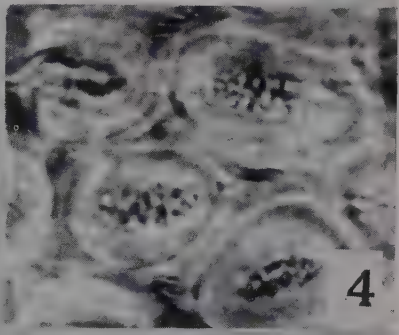
FIG. 5. Same specimen as shown in Figs. 1 and 2, but with varying degrees of degradation of the cell wall previous to silification. Ground section. ×732.

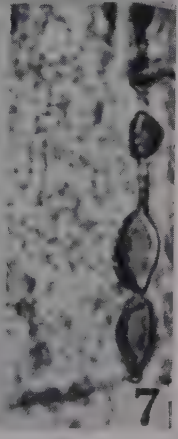
FIG. 6. Tangential longitudinal section of same specimen as shown in Fig. 4. The beaded structure of the more resistant primary wall is preserved as an organic residue, consisting of modified lignin and embedded in silica. Ground section. ×225.

FIG. 7. Same as Fig. 6, except more highly magnified. Ground section. ×860.

PLATE V







EXPLANATION OF THE ILLUSTRATIONS

PLATE VI. FIG. 1. Portion of root of *Juncus* sp. isolated from postglacial peat. Age approximately 4000 to 5000 years. The heavily lignified fibrous and conductive tissue in the center of the root has been largely degraded, whereas the delicate unlignified epidermal structures are preserved. ×132.

FIG. 2. Root epidermis of *Scirpus* sp. from same peat. Note preservation of epidermal cells. ×126.

FIG. 3. Root epidermis of *Carex* sp. from same peat. ×126.

FIG. 4. Root tip of unidentified monocotyledonous root from same peat. Note preservation of minute structural details of root cap. Treated with acidified sodium chlorite. ×126.

FIG. 5. Cells of a root apex meristem from the same peat showing preservation of primary cell walls and the residue of cell contents. Thin section of peat, unstained. ×500.

FIG. 6. Root epidermis of *Carex* sp. showing preservation of unlignified primary walls of epidermal cells. ×126.

PLATE VI